Thesis/
Reports
Hayward,
G. D.

Boreal Owl Population Trend, Habitat Use, and Dispersal in 1998: Final Report

COOP AGREEMENT

UNIV OF WYOMING

FINAL REPORT FOR RESEARCH AGREEMENT
#RMRS-98568-RJVA
"Response of Red-Backed Voles to Landscape Configuration: Applications for Forest Management"
UNIVERSITY OF WYOMING
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Response of Red-Backed Voles to Landscape Configuration in 1998: Final Report

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This research was supported in part by funds provided by the Rocky Mountain Research Station, Forest Service, U.S. Department of Agriculture.

Introduction

This project was designed to apply the concepts of movement analysis in determining the effects of landscape heterogeneity on the dispersal and abundance of red-backed voles in subalpine conifer forests. The behavior of individual voles was examined by documenting vole movement pathways and conducting extensive live trapping in heterogeneous environments.

This is a new approach to the long-standing problem of determining habitat preference and will yield unique insights not gained by more traditional methods. Evidence suggests that large-scale population dynamics result from the collective non-random movements of individual animals responding to small scale patterns (Crist and Wiens, 1995; Gross et al., 1995; Wiens et al., 1993b; Van Horne, 1982). Moreover, animal movements can provide important insights regarding the consequences of landscape heterogeneity, since their combined effects have a potentially significant impact on ecosystem structure and function (Gross et al., 1995; Gessaman and MacMahon, 1984). Therefore, the search for a mechanistic understanding of population dynamics requires an understanding of individual movements. This is not to say that population dynamics can be studied on the basis of individual actions considered in isolation. Indeed, individual behavior can vary in ways inconsistent with population level trends (Crist and Wiens, 1994). Rather, population characteristics are the collective expression of many individual responses to population level forces.

Perhaps the most critical aspect of movement analysis is identifying how movements are affected by habitat boundaries, because boundaries represent the interface of patches with different structure and function. Movement of matter and energy across boundaries will influence characteristics of both patches. Furthermore, patches represent sites with different habitat characteristics, so decisions made by animals at boundaries represent important choices in the context of habitat selection and use. More specifically, a critical question asks: How do movements in favorable habitat differ from those in unfavorable habitat, and how do those movements change across the ecotone separating those habitats? Applying movement analysis to this question will yield insights not obtained via traditional methods, because unlike the more common phenomenological approaches, the movement-based analysis of boundary dynamics addresses the mechanisms underlying the alteration of forest mammal activity in response to landscape changes (Wiens, 1992).

Subalpine Conifer Forests

The habitat of interest in this study is subalpine spruce-fir forest, which represents a climax community in high elevation montane regions in the Rocky Mountains (Knight, 1994b). The dominant tree species in these forests are Engelmann spruce (*Picea engelmannii*) and subalpine fire (*Abies lasiocarpa*). In mature spruce-fir forests of the southern Wyoming mountains, a large portion of the understory canopy consists of shade-tolerant *A. lasiocarpa* seedlings and ground vegetation is dominated by dwarf huckleberry (*Vaccinium scoparium*). Production of fungi and lichen is often high in these late seral coniferous forests (Clarkson and Mills, 1994; Esseen et al., 1996). Another characteristic of mature and old-growth spruce-fir forest is an abundance of course woody debris (CWD), which forms habitat for forest organisms and contributes to fungus and lichen production (Lesica et al., 1991; Corn and Raphael, 1992; Merritt, 1981; Amaranthus et al., 1994). Mature spruce-fir forests have relatively simple small mammal communities compared to other montane vegetation types. The field data from this project suggest that the southern red-backed vole (*Clethrionomys gapperi*) is by far the most abundant small mammal species in the selected spruce-fir stands.

Large-scale natural disturbances are infrequent and have long-lasting effects in subalpine spruce-fir assemblages (Knight, 1994a). For example, the fire return interval is usually quite long (on the order of 200 years; Velben et al., 1994), and the regeneration time of old-growth spruce-fir following disturbance can take 150 to 300 years or more (Knight, 1994a; Veblen, 1989). Moreover, stand replacement disturbance of any sort has severe and long-lasting impact on subalpine spruce-fir forests, because these forests exhibit very long successional development, low growth, and relatively low productivity, particularly at high elevations (Knight, 1994a; Peet, 1989).

Southern Red-Backed Voles (*Clethrionomys gapperi*)

Southern red-backed voles generally weigh from 6 to 42 grams, measure 116 to 172 mm nose to tail length, and occupy a home range of 0.01 to 0.5 hectares (Burt and Grossenheider, 1980; Merritt, 1981). *C. gapperi* is an opportunistic omnivore feeding on fungi, green vegetation, seeds, and some insects depending on geographic and seasonal availability (Burt and Grossenheider, 1980; Merritt, 1981), but the bulk of their diet in the central Rocky Mountains usually consists of fungal sporocarps and green vegetation such as *V. scoparium* (Maser, 1998). *C. gapperi* are active year-round and appear to have short duration cyclic daily activity patterns, but these patterns do not appear consistent or predictable. Some studies have shown a moderately diurnal pattern with peak activity in the morning (Stebbins, 1984). Others sources have reported a nocturnal pattern (Baron and Pottier, 1977 in Merritt, 1981). Still others have shown no diurnal or nocturnal preference, but rather short activity periods occurring throughout the day and night (Brown, 1971 in Merritt, 1981). Daily activity patterns are likely related to season, habitat, and latitude, but there is dissension as to the nature of this relationship (Merritt, 1981; Stebbins, 1984; Herman, 1977 in Merritt, 1981; Clark and Stromberg, 1987). Thus, they are not clearly diurnal or nocturnal, but may be active anytime of the day or night on a cyclic activity pattern of 1 to 7 active periods per 24-hours (Merritt, 1981; Gilbert et al., 1986).

C. gapperi was chosen for this study for several reasons. First, it is a crucial species in subalpine coniferous forests, because it is the primary prey for many small carnivores, including boreal owls (*Aegolius funereus*), great gray owls (*Strix nebulosa*), and American martens (*Martes anericana*), all of which are habitat specialists and potentially prey limited species (Hayward and Verner, 1994; Ruggerio et al, 1994). Second, sporocarps of hypogeous mycorrhizal fungi comprise a potentially significant portion of vole diet (Maser, 1998; Ure and Maser, 1982). Thus, through their consumption of mycorrhizal fungi and subsequent dispersal of fungal spores, red-backed voles may be important in spruce-fir forest establishment and productivity (Pastor et al., 1996; Rhoades, 1986). An increased understanding of red-backed voles and their movement and habitat selection characteristics is therefore of value in the management of the subalpine coniferous forests.

Third, *C. gapperi* is a widely distributed species whose general habitat preferences are fairly well defined, making it an ideal species for evaluating the effectiveness of movement analysis as a metric for habitat preference. Red-backed voles are found across northern North America in mesic forests (Merrit, 1981). Depending on region, red-backed voles may inhabit coniferous, deciduous, or mixed forest, but in the central Rocky Mountains, they are largely associated with coniferous forests, particularly mature spruce-fir forests (Hayward, 1994; Hayward et al, 1993; Scrivner and Smith, 1984; Nordyke and Buskirk, 1991; Vickery and Rivest, 1992). The presence of vegetative cover (i.e., overstory canopy), coarse woody debris, and proximity to water appear to be factors determining habitat selection by *C. gapperi* (Merritt, 1981; Nordyke and Buskirk, 1991; Wywialowski, 1987). Red-backed voles are sensitive to habitat disturbance, as their abundance has been shown to respond negatively to forest alteration via burning and/or clearcutting (Merritt, 1981; Martell, 1984; Medin, 1986; Sekgororoane and Dilworth, 1995). They also appear to be somewhat boundary shy, preferring to inhabit the interior of spruce-fir patches (Kirkland et al., 1985), although a recent study has suggested they may be less edge averse than previously thought (Hayward et al., 1999).

Methods

Field Methods - Sites

This study was conducted in the Snowy Range Mountains of the Medicine Bow National Forest in Southeastern Wyoming. The study area was located in Carbon County, Wyoming and is part of the Laramie Ranger District. It lies approximately 64 kilometers (40 miles) west of the University of Wyoming campus in subalpine conifer forest at an elevation of between 3,050 and 3,200 meters (10,000 and 10,500 feet) above sea level. The approximate Universal Transverse Mercator (UTM) coordinates for the area are 4584000 North and 398000 East. Access was achieved on foot from Forest Road 101 (Sand Lake Road) about 7 miles north of State Highway 130 (Snowy Range Road).

An additional site was selected in the Fool Creek Drainage of the Fraser Experimental Forest in central Colorado. Fraser Experimental Forest is located near the town of Fraser, Colorado and is administered by the Rocky Mountain Forest and Range Experiment Station in Fort Collins, Colorado. This site was visited in 1997, but logistical constraints precluded its inclusion in 1998. Thus, one summer of capture data is available for the Fraser

site, but has not been incorporated into analysis at this point. Attempts will be made to incorporate the Fraser data into future capture analyses. Unfortunately, the Fraser site will not factor into movement analyses since no movement data has been collected from that location.

Sites were selected for trap placement and movement pathway collection based on a combination of forest and non-forest characteristics. Each site was chosen such that the forest component manifested qualities of old-growth subalpine spruce-fir forest. Vertical structure in these forests was complex, including trees of many different size classes. Overstory[1] canopy was generally dominated by Engelmann spruce (*Picea engelmannii*), with subalpine fir (*Abies lasiocarpa*) often occurring as a co-dominant. The understory canopy consisted mainly of immature *A. lasiocarpa* and ground cover was almost entirely dwarf huckleberry (*Vaccinium scoparium*). Course woody debris was abundant and varied greatly in size and age.

The nature of the study required that forested areas be directly adjacent to areas with past harvest activities, so harvests of approximately the same age (20 to 30 years old) were located next to identified old-growth stands. The harvests selected had between 5 and 20 percent canopy cover, as opposed to more than 40 percent in the adjacent forests. Canopy in harvest units consisted almost entirely of *A. lasiocarpa* seedlings and saplings from 4 to 20 feet tall, with occasional occurrences of *P. engelmannii* and lodgepole pine (*Pinus contorta*). The understory canopy was equally sparse, being comprised of the lower branches of the above noted immature conifers. Ground vegetation was more varied than in the forests, consisting of a variety of graminoids and forbs. .

Other site selection criteria were geographic proximity and topographic variation. Proximal sites were selected in order to minimize inter-site environmental variation and areas trapped all had slopes that were relatively consistent with less than a 7 percent grade.

Field Methods - Trapping Grids

Based on the above criteria, three sites were selected for study. At each site an "abundance grid" of 200 traps was established with dimensions of 10 traps by 20 traps spaced 10 meters apart. Each grid was established such that its long axis was approximately bisected by the forest-cut boundary (Figure 1). In this way *C. gapperi* distribution was obtained along a gradient through each habitat type (i.e., forest interior, harvest interior and edge). Traps were checked twice daily, once in the early morning and once in the late evening. Captured animals were identified to species, marked with unique ear tags, weighed, sexed, measured (i.e., tail, body and hind foot length) and released at the capture site. The date, time and trap location of each capture was also recorded, as well as general observations on the physical condition of the animal. Tripped or broken traps that contained no captured animals were recorded, and this data was used to modify trapping effort.

Field Methods - Movement Paths

Approximately one movement path was recorded during each day the abundance grids were being checked using a modification of the fluorescent powder technique presented by Lemen and Freeman (1985) and subsequently used in microhabitat and movement-based studies of small mammals (Stapp, 1997; Barnum et al, 1992; Graves and Wolf, 1988). Only previously uncaught voles classified as adults in good physical condition were tracked to avoid bias induced by age, health, and animals who had become accustomed to traps. Voles were selected for tracking such that an approximately equal number of paths were obtained in the forest and harvested areas. To prevent nearby traps from influencing movement pathways, all traps in a 20 to 30 meter radius of the release point were removed. Each vole to be tracked was covered with fluorescent powder (Radiant Color, Richmond, California and Day-Glo Color Corporation, Cleveland, Ohio) and released at the capture location once the nearby traps were removed. Powder was applied to the animals' fur with a course paint brush to minimize inhalation of the powder by voles. With the exception of two animals, all voles were powdered and released in the morning. In the event that two powdered voles were released in the same vicinity, each vole was given a different colored powder to avoid confusion if the tracks should overlap. Some voles were tracked before the abundance grids were established (three small grids of 4X5 traps each were set up and checked daily immediately prior to trapping on the large, abundance

1 For the purposes of all vegetation analyses in this study, overstory canopy was defined as canopy cover occurring greater than one meter above the forest floor and consisted primarily of mature Engelmann spruce and subalpine fir. Understory canopy was defined as canopy occurring between approximately ten centimeters and one meter from the forest floor and consisted primarily of subalpine fir seedlings and saplings. Any vegetation below ten centimeters in height was classified as ground cover.

grids). Animals caught in these grids were tracked as noted. When the abundance grids were fully established, these small grids became part of the larger grids.

As powdered voles moved through the forest, bits of powder were sloughed off onto objects they came in contact with (e.g., vegetation, logs, debris), leaving a trail of powder which could be followed and documented. Paths were marked the night after the powdered voles were released. Technicians returned to the release point at dusk and illuminated the area with a portable ultra violet light (Ultra-Lum, Inc., Carson, California), which caused the trail of powder to glow. Beginning with the release point, sequentially numbered flags were placed every 40 cm along the trail. Note was made whenever a vole entered a hole or stopped to clean itself, the latter event being discernible by a dense patch of powder shed while the animal was cleaning.

Once flags were placed, technicians returned during daylight and documented the paths by recording the ground cover in which each flag was located[2], the presence or absence of overstory canopy above each flag, the distance of each flag to the nearest log, the compass bearing of the path between consecutive flags, and the proportion of the intervening path intersecting each ground cover category. Bearings between consecutive flags were taken using a Suunuto MD-1 compass mounted to a 60 cm long wooden stick. The stick was positioned such that one edge contacted both flags, allowing an accurate assessment of the direction the vole was heading during each 40 cm segment. The same stick was graduated in centimeters and decimeters, thus providing a scale which was used to estimate the proportion of each 40 cm segment which intersected each ground cover type.

Field Methods - Vegetation Surveys

At all 200 trap locations in each abundance grid, the position of the trap was recorded (i.e., the ground-cover type at the trap location and the distance of the trap from the forest/harvest edge.). To establish a more complete picture of site structure, stratified random sampling was used to select 30 trap locations evenly distributed throughout each grid. At each of these locations several vegetation features were measured and recorded, including ground cover, basal area, canopy cover, course woody debris, and distance from the forest/harvest boundary.

Percent ground cover in each of the standardized categories was visually estimated in a one meter radius ring centered on a point located randomly within two meters of the trap. These estimates were validated by conducting a Daubenmyer plot analysis at a subset of the points and comparing the results to our visual method. Specifically five Daubenmyer plots were sampled per location. One was placed at the sample point and the other four will be located at cardinal directions along a one meter radius circle centered on the trap.

Basal area was estimated at each point using a modified Bitterlich Variable Plot Method with a basal area factor of 20 (Barbour et al., 1987). To estimate percent of overstory canopy coverage, a 30 meter line intercept transect was placed at each trap location, oriented along the topographic contour. Technicians walked each transect and recorded points at which it intersected the overstory canopy, using a three meter rod to site distant foliage boundaries. To estimate the percent of understory canopy cover, coverage of a one meter radius ring centered on the point was estimated as falling into one of eight categories based on visual examination (less than 10 percent cover, 10 to 25 percent cover, 26 to 50 percent cover, 50 to 75 percent cover, and greater than 75 percent cover). The ground-cover type in which the sample point was located was also noted.

Two methods were used to quantify course woody debris on the study sites. First, the density of CWD was estimated by counting all logs within five meters of the sample point. Second, the distance from the sample point to the nearest log was measured with a 100 meter tape.

In order to compare vegetation along pathways with the site at large, each of the above metrics was also recorded along the movement pathways. Using the same methods noted above, percent ground cover, basal area, percent canopy cover, and CWD metrics were recorded a five meter intervals along the paths, which corresponds to roughly every twelfth flag. In addition, the position of each flag in each pathway was recorded, as was whether or not that flag was under overstory and understory cover.

Analysis Methods - Capture Data

Preliminary descriptive analyses of the capture records were conducted using standard spreadsheet software (Microsoft Excel 95). Specific analyses included: calculation of the proportion of captures by species; calculation

2 Ground cover categories were identical to those for vegetation analysis: *V. scoparium*, grasses and other herbaceous vegetation, moss, shrubs (including low-growing conifer seedlings and saplings), tree boles, bare ground (including fine, non-woody litter), course woody debris (diameter 15 cm and length 1 m, also referred to as logs), and fine woody debris (woody material not meeting the size requirements for CWD).

of the proportion of captures in each of three major habitats along the forest-harvest gradient (i.e. clearcut, edge, and forest); and calculation of the proportion of captures in each of seven microhabitat types (noted below). All captures were analyzed relative to trapping effort.

For the habitat analysis, edge was defined as a twenty meter strip centered on the perceived boundary between intact forest and harvested area, which was determined by locating the stumps of harvested trees. Thus, any trap within 10 meters of this boundary was considered to be in the edge. For the microhabitat analysis, microhabitat types corresponded roughly to the ground cover categories recorded during vegetation survey, with one exception: the ground cover categories of bare ground, moss, and rock were combined into a single microhabitat type, because they all represent open areas of low occurrence from which *C. gapperi* are not expected to derive value. Thus, the microhabitat types included open area (bare ground, moss, or rock), course woody debris, fine woody debris, *V. scoparium*, grasses and other herbaceous vegetation, shrubs, and tree boles.

Further analyses of data from the abundance grids will be conducted using the Capture Program, resulting in abundance estimates for voles in the forest and harvest habitats being studied.

Analysis Methods - Statistical Comparisons and Models

Data obtained from vegetation surveys and pathways is still being compiled, so analysis incorporating these data sets has not yet been undertaken. The raw data will be entered and compiled during the winter of 1998 and early spring of 1999. Once this is done, analysis will proceed in three phases: 1) conducting descriptive analyses and statistical comparisons of movement paths; 2) constructing a spatially explicit model of vole movement parameterized by the empirical data; and 3) performing iterative re-valuation of the model and path analyses. By the established completion date for this project (roughly October 1999) we expect to complete phase 1 and have a simple phase 2 model developed and tested. This information will form the foundation for phase three, which will likely be an ongoing process requiring additional support.

While compiling data, we have begun preliminary work on phase one, wherein paths will be analyzed by comparing habitat variables recorded along the paths with those recorded at random over the sites. These analyses will include, but not be limited to, comparing the canopy cover of paths to the canopy cover of random transects; comparing the proportions of ground cover categories through which paths lead to those expected based on site cover estimates; comparing the proximity of pathways to downed logs to the random proximity expected from CWD estimates; and comparing the percent of flags in each cover type to the percent of random points in each cover type. These analyses will largely be conducted using standard ANOVA and multivariate techniques. Further, path metrics such as mean turning angles and estimates of toruosity will be derived and correlated with general habitat characteristics. Based on these analyses we expect to see more complex pathways in habitats which are preferred, and thus used, by *C. gapperi.* Since red-backed voles have been shown to associate with old-growth characteristics, such as course woody debris, there should be a general trend in path toruosity such that paths in the forest settings are consistently more convoluted that those in the harvest settings.

Results and Discussion

Capture Data

Capture data for all sites are summarized Table 13. *C. gapperi* were by far the most abundant small mammal captured, comprising more than 75 percent of all captures across habitat types and about 90 percent of captures in the forests. Other taxa captured, in rough order of decreasing frequency, were long tailed voles (*Microtus longicaudus*), Mountain phyenacomys (*Phyenacomys intermedius*), masked shrews (*Sorex cinereus*), deer mice (*Peromyscus maniculatus*), and one ermine (*Mustela erminea*).

Based solely on the capture data, red-backed voles exhibited a clear preference for the forested habitat on each site. Further, the harvest boundary appeared quite sharp to *C. gapperi*, since very few red-backed voles were captured more than 10 meters into the clearcuts and many were captured in the forest up to its edge (Figure 1). In fact, at two of the three sites, *C. gapperi* were captured as or more readily in the edge habitat than in the interior forest and most of these captures were on the forest side of the boundary For a species often described as an interior obligate, this is an interesting finding which supports other research being conducted in this laboratory (Hayward, 1999).

3 The Fraser, Colorado site is included in the table, but subsequent analyses focus on the Medicine Bow sites only.

C. gapperi showed a preference for microhabitats with ground cover dominated by course woody debris, as evidenced by the fact that they were captured nearly twice as frequently in traps placed near logs than any other microhabitat feature (Figure 2). In contrast, red-backed voles avoided microhabitats dominated by grasses and other herbaceous species. Captures per trap-day in traps located in grasses and herbs were less than a third of those in the next lowest microhabitat type (*V. scoparium*) and over ten times fewer than in course woody debris. This was in part a reflection of their avoidance of the harvested areas, since grass-dominated herbaceous ground vegetation was most prevalent in the clearcuts and gave way to *V soparium* in the forested areas. No preferences appeared for any of the other cover types, each of them capturing voles with comparable frequency.

Field Observations

Most of the data collected on movement pathways have not been digitized and therefore have not been analyzed. Despite this fact, several preliminary statements can be made based on field observations.

Voles responded to the boundary between forested and harvested areas. Based on captures and observation of vole pathways, voles seemed to rarely cross the boundary from forest into harvest. Further, when doing so they did not seem to travel much more than 10 meters away from the forest edge. On the other hand, voles seemed to cross readily back into the forest. Several voles that we captured a short distance into the harvested area and subsequently moved back into the forest while we tracked them. This suggests a differential edge permeability to voles, with voles more likely to cross the forest-harvest boundary when located in the harvest than when located in the forest.

It appears that cover within a few meters of the ground affected vole movement more than overstory canopy, since voles appeared to move more often under short cover (i.e., course woody debris, low-growing shrubs, and fine woody debris) than not. Course woody debris seemed to be the preferred avenue of transport, which makes biological sense as it often forms an interconnected grid of cover over fairly large areas. However, the importance of short cover was most evident in timber harvests with sparse course woody debris. In such cases, conifer seedlings and saplings were the dominant short cover. Voles moved in complex patterns under the dense lower branches of these seedlings and saplings while traversing the open areas between seedling stands in a highly directional, linear fashion. I suspect these observations to be born out by correlating path totuosity with ground cover and by seeing an inordinate length of pathways occurring near course woody debris and shrubs.

This study was designed to investigate two dimensional space use by voles, but anecdotal information was also gained on vertical habitat use. After following numerous tracks, it is apparent that voles use the vertical structure of the forest up to about one meter from the ground. Paths were frequently followed up logs and root balls to this height. Also, in harvested areas where most activity seemed to occur under conifer seedlings and saplings, voles often climbed into and moved among the lower branches. Further, on a few isolated occasions, voles were observed climbing the trunks of saplings to a height of greater than two meters. This does not suggest that voles are arboreal, merely that they make limited use of the near-ground vertical structure of their environment.

Acknowledgements

Several organizations and individuals contributed to this project. Specifically I would like to thank Dr. Stanley Anderson and the Wyoming Cooperative Fish and Wildlife Research unit for providing financial and technical support throughout the project. Additional funding was provided by the Max McGraw Wildlife Foundation, the Rocky Mountain Forest and Range Experiment Station, and the University of Wyoming Agricultural Experiment Station. For sites in the Medicine Bow Forest, extensive field support was provided by Joe Harper, Jenny Newton, and the Laramie Ranger District of the United States Forest Service, while the Rocky Mountain Forest and Range Experiment Station provided housing at the Fraser site. Additional thanks are extended to members of the faculty, staff, and student body of the University of Wyoming Departments of Botany and Zoology and Physiology for their technical and moral support. Particular thanks go to Shelli Dubay, Amanda Hale, Dr. Dennis Knight, Nicole Korfanta, Nathan Nibbelink, Rich Russell, Kimberly Simpson, and Heather Struempf.

References

Amaranthus, M.; Trappe, J.M.; Bednar, L.; Arthur, D. 1994. Hypogeous fungal production in mature Douglas-fir forest fragments and surrounding plantations and its relation to coarse woody debris and animal mycophagy. Canadian Journal of Forest Research. 24(11):2157-2165.

Barbour, M. G., J. H. Burk, and W. D. Pitts. 1987. Terrestrial Vegetation Ecology, second edition. Benjamin/Cummings Publishing Company, Inc., Menlo Park, California.

Barnum S. A., C. J. Manville, J. R. Tester, and W. J. Carmen. 1992. Path selection by peromyscus leucopus in the presence and absence of vegetative cover. Journal of Mammalogy, 73(4):797-801.

Brown, E. B. 1971. Some aspects of the ecology of the small, winter-active mammals of a field and adjacent woods in Itasca State Park, Minnesota. Ph.D. dissertation, University of Minnesota, Minneapolis. 193 p.

Burt, W.H.; Grossenheider, R.P. 1980. A field guide to the mammals: North America north of Mexico. New York, NY: Houghton Mifflin Company.

Clark T. W. and M. R. Stromberg. 1987. Mammals in Wyoming. University of Kansas, Museum of Natural History, Public Education Series No. 10. 314 p.

Clarkson, D.A.; Mills, L.S. 1994. Hypogeous Sporocarps in Forest Remnants and Clearcuts in Southwest Oregon. Northwest Science. 64(4):259-265.

Corn, J.G.; Raphael, M.G. 1992. Habitat characteristics at marten subnivean access sites. Journal of Wildlife Management. 56(3):442-448.

Crist, T.O.; Wiens, J.A. 1995. Individual movements and estimation of populations size in darkling beetles (Coleoptra: Tenebrionidae). Journal of Animal Ecology. 64:733-746.

Crist, T.O.; Wiens, J.A. 1994. Scale effects of vegetation on forager movement and seed harvesting by ants. Oikos. 69(1):37-46.

Crist, T.O.; Guertin, D.S.; Wiens, J.A.; Milne, B.T. 1992. Animal movement in heterogeneous landscapes: An experiment with Eleodes beetles in shortgrass prairie. Functional Ecology. 6(5):536-544.

Esseen, P.A.; Renhorn, K.E.; Pettersson, R.B. 1996. Epiphytic lichen biomass in managed and old-growth boreal forests: Effect of branch quality. Ecological Applications. 6(1):228-238.

Gessaman, J.A.; MacMahon, J.A. 1984. Mammals in ecosystems: their effects on the composition and production of vegetation. Acta Zool Fennica. 172:11-18

Gilbert, B.S.; Cichowski, D.B.; Talarico, D; Krebs, C.J. 1986. Summer activity patterns of three rodents in the southwestern Yukon (Canada). Arctic. 39(3):204-207.

Graves, S. M. and J. O. Wolf. 1988. Use of ground and arboreal microhabitats by *Peromyscus leucopus* and *Permyscus maniculatus*. Canadian Journal of Zoology, 66:277-278.

Gross, J.E.; Zank, C.; Hobbs, T.H.; Spalinger, D.E. 1995. Movement rules for herbivores in spatially heterogeneous environments: responses to small scale pattern. Landscape Ecology. 10(4):209-217.

Hayward, G. D., S. H. Henry, and L. F. Ruggiero. 1999. Response of red-backed voles to recent patch cutting in subalpine forest. Conservation Biology, 13:1-10. In press.

Hayward, G.D.; Verner, J. eds. 1994. Flammulated, Boreal, and Great Gray Owls in the Unites States: A Technical Conservation Assessment. USDA Forest Service, General Technical Report RM-253.

Hayward, G.D.; Hayward, P.H.; Garton, E.O. 1993. Ecology of Boreal owls in the northern Rocky Mountains, USA. Wildlife Monographs. 0(124):1-59.

Herman, T. B. 1977. Activity patterns and movements of sub-arctic voles. Oikos, 29:434-444.

Johnson, A.R.; Wiens, J.A.; Milne, B.T.; Crist, T.O. 1992. Animal movements and population dynamics in heterogeneous landscapes. Landscape Ecology. 7(1):63-75.

Kirkland, G.L., Jr.; Johnston, T.R., Jr.; Steblein, P.F. 1985. Small mammal exploitation of a forest clearcut interface. Acta Theriologica. 30(9-20):211-218.

Knight, D.H. 1994a. Dynamics of Subalpine Forests. Hayward, G.D.; Verner, J. eds. Flammulated, Boreal, and Great Gray Owls in the Unites States: A Technical Conservation Assessment. USDA Forest Service, General Technical Report RM-253.

Knight, D.H. 1994b. Mountains and Plains: The Ecology of Wyoming Landscapes. Yale University Press. Hew Haven, Connecticut.

Lemen, C. A., and P. W. Freeman. 1985. Tracking mammals with fluorescent pigments: a new technique. Journal of Mammalogy, 66(1):134-135.

Lesica, P.; McCune, B.; Cooper, S.V.; Hong, W.S. 1991. Differences in lichen and bryophyte communities between old-growth and managed second-growth forests in the Swan Valley, Montana. Canadian Journal of Botany. 96(5):321-330.

Martell, A.M. 1984. Changes in small mammal communities after fire in northcentral Ontario (Canada). Canadian Field Naturalist. 98(2):223-226.
Maser, C. 1998. Personal telephone contact with Douglas A. Keinath in May, 1998.
Medin, D.E. 1986. Small mammal responses to diameter-cut logging in an Idaho (USA) Douglas fir forest. U.S. Forest Service Research Note Int. 0(362):1-6.
Merritt, J.F. 1981. Clethrionomys gapperi. Mammalian Species. 146:1-9.
Nordyke, K.A.; Buskirk, S.W. 1991. Southern red-backed vole, Clethrionomys gapperi, populations in relation to stand succession and old-growth character in the central Rocky Mountains. Canadian Field Naturalist. 105(3):330-334.
Pastor, J; Dewey, B; Chrisain, D.P. 1996. Carbon and nutrient mineralization and fungal spore composition of fecal pellets from voles in Minnesota. Ecography. 19(1):52-61.
Peet, R.K. 1989. Forests of the Rocky Mountains. Barbour M.G.; Billings, W.D. eds. North American Terrestrial Vegetation. New York: Cambridge University Press; pp. 64-103
Rhoades, F. 1986. Small mammal mycophagy near woody debris accumulations in the Stehekin River Valley, Washington (USA). Northwest Science. 60(3):150-153; 1986.
Ruggiero, L.F.; Aubry, K.B.; Buskrirk, S.W.; Lyon, J.L.; Zielinski, W.J. 1994. The Scientific Basis for Conserving Forest Carnivores: American Martin, Fisher, Lynx, and Wolverine in the Western United States. USDA Forest Service, General Technical Report RM-254.
Scrivner, J.H.; Smith, H.D. 1984. Relative abundance of small mammals in 4 successional stages of spruce-fir forest in Idaho (USA). Northwest Science. 58(3):171-176.
Sekgororoane, G.B.; Dilworth, T.G. 1995. Relative abundance, richness, and diversity of small mammals at induced forest edges. Canadian Journal of Zoology. 73(8):1432-1437.
Stebbins, L. L. 1984. Overwintering activity of Peromyscus maniculatus, Clethrionomys gapperi, C. rutilus, Eutamias amoenus, and Microtus pennsylvanicus. Special publication of the Carnegie Museum of Natural History, No. 10.
Stapp, P. 1997. Community structure of shortgrass prarrie rodents: competition or risk of intraguild predation? Ecology. 78(5):1519-1530.
Ure, D.C.; Maser, C. 1982. Mycophagy of red-backed voles in Oregon and Washington. Canadian Journal of Zoology. 60:3307-3315.
Van Horne, B. 1982. Niches of adult and juvenile deer mice (Peromyscus manticulatus) in seral stages of coniferous forest. Ecology. 63:992-1003.
Veblen, T.T.; Hadley, K.S.; Nel, E.M.; Kitzberger, T.; Villalba, R. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. Journal of Ecology. 82(1):125-135.
Veblen, T.T.; Hadley, K.S.; Reid, M.S.; Rebertus, A.J. 1989. Blowdown and stand dynamics in a Colorado (USA) subalpine forest. Canadian Journal of Forest Research. 19(10):1218-1225.
Vickery, W.L.; and Rivest, D. 1992. The influence of weather on habitat use by small mammals. Ecography. 15(2):205-211.
Wiens, J.A.; Crist, T.O.; Milne, B.T. 1993a. On quantifying insect movements. Environmental Entomology. 22(4):709-715.
Wiens, J.A.; Stenseth, N.; Van Horne, B.; Ims, R.A. 1993b. Ecological mechanisms and landscape ecology. Oikos. 66:369-380.
Wiens, J.A. 1992. Ecological Flows across landscape boundaries: a conceptual overview. Hansen, A.J.; diCastri, F. eds. Landscape boundaries: consequences for biotic diversity and ecological flows. Springer-Verlag. New York, NY; pp. 217-235.
Wywialowski, A.P. 1987. Habitat structure and predators: Choices and consequences for rodent habitat specialists and generalists. Oecologia. 72(1):39-45.

Table 1: Summary of Capture Data

Grid	Year	Species	Cut	Edge	Forest	Total
FC2	97	CG	9	8	16	33
		PM			3	3
		TM	4	3	1	8
	97 Total		13	11	20	44
FC2 Total			13	11	20	44
MB1	97	CG		11	36	47
	97 Total			11	36	47
	98	CG		11	40	51
		PM		1	1	2
		SC		2	5	7
	98 Total			14	46	60
MB1 Total				25	82	107
MB2	97	CG	5	8	18	31
		Ermine	1			1
		OtherVoles	16	4	1	21
	97 Total		22	12	19	53
	98	CG	8	6	9	23
		OtherVoles	11	1		12
		SC	2	4	2	8
	98 Total		21	11	11	43
MB2 Total			43	23	30	96
MB3	98	CG		4	26	30
		PM			1	1
		SC	1	1	4	6
	98 Total		1	5	31	37
MB3 Total			1	5	31	37
Grand Total			57	64	163	284

This table is a summary of the capture data from two summers of field work. It shows unique captures (i.e., recaptured animals are not included) by year (1997 or 1998), field site (FC1, MB1, MB2, and MB3), and habitat category (Cut, Edge, and Forest). The MB1, MB2, and MB3 sites were in the Medicine Bow Mountains of Wyoming and site FC2 was in the Fraser Experimental Forest of Colorado. "Cut" is defined as any location greater than 10 meters into harvested areas and "Forest" is defined as any location greater than 10 meters into forest, so the "Edge" is a 20 meter strip centered on the forest-harvest boundary. Species codes are: CG is *Clethrionomys gapperi*; PM is *Peromyscus maniculatus*; TM is *Tamias minimus*; SC is *Sorex cinereus*; Ermine is *Mustela erminea*; and Other voles include *Microtus longicaudus* and *Phyenacomys intermedius.*